Underestimated ecosystem carbon turnover time and sequestration under the steady state assumption: a perspective from longterm data assimilation

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Running head: underestimated turnover time at equilibrium

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Abstract

It is critical to accurately estimate carbon (C) turnover time as it dominates the uncertainty in ecosystem C sinks and their response to future climate change. In the absence of direct observations of ecosystem C losses, C turnover times are commonly estimated under the steady-state assumption (SSA), which has been applied across a large range of temporal and spatial scales including many at which the validity of the assumption is likely to be violated. However the errors associated with improperly applying SSA to estimate C turnover time and its covariance with climate as well as ecosystem C sequestrations have yet to be fully quantified. Here we developed a novel model-data fusion (MDF) framework and systematically analyzed the SSA-induced biases using time-series data collected from 10 permanent forest plots in the eastern China monsoon region. The results showed that (1) the SSA significantly underestimated mean turnover times (MTTs) by 29%, thereby leading to a 4.83-fold underestimation of the net ecosystem productivity (NEP) in these forest ecosystems, a major C sink globally; (2) the SSA-induced bias in MTT and NEP correlates negatively with forest age, which provides a significant caveat for applying the SSA to young-aged ecosystems; and (3) the sensitivity of MTT to temperature and precipitation was 22% and 42% lower, respectively, under the SSA. Thus, under the expected climate change, spatiotemporal changes in MTT are likely to be underestimated, thereby resulting in large errors in the variability of predicted global NEP. With the development of observation technology and the accumulation of spatiotemporal data, we suggest estimating MTTs at the disequilibrium state via long-term data assimilation, thereby effectively reducing the uncertainty in ecosystem C sequestration estimations and providing a better understanding of regional or global C cycle dynamics and C-climate feedback.

Introduction

The terrestrial carbon (C) cycle is among the largest uncertainties affecting global C-climate feedback (Le Quéré *et al*., 2018). Ecosystem C input (gross primary productivity, GPP) and C mean turnover time (MTT) are two key factors in determining the C sequestration capacity of terrestrial ecosystems (Xia *et al*., 2013; Luo *et al*., 2017). Terrestrial GPP has been well studied and exhibits a relatively strong convergence in global modelling studies (Anav *et al*., 2013), whereas the C turnover time has become the dominant uncertainty in terrestrial ecosystem C sequestration and its response to climate change (Carvalhais *et al*., 2014; Friend *et al*., 2014; He *et al*., 2016). Therefore, accurately quantifying the ecosystem MTT and its relationship with climate is crucial for understanding the present and future C budget dynamics in terrestrial ecosystems.

Ecosystem MTT refers to the average time required for atmospheric CO_2 to enter the ecosystem via plant photosynthesis and return to the atmosphere via C loss pathways, such as ecosystem respiration (RE) and fire (Barrett, 2002). As the current understanding of these C cycle processes is mainly based on first-order kinetics (Manzoni and Porporato, 2009), MTT is commonly defined as the ratio of the C pool to the flux (Bolin and Rodhe, 1973; Friedlingstein *et al*, 2006; Koven *et al*., 2015). Therefore, the flux used for MTT estimation (i.e., influx or efflux), the state of C pools, as well as the C allocation and turnover rates that control the C flow in various pools, are all key states and processes that collectively determine for the overall ecosystem turnover time (Sitch *et al*., 2003; Trumbore *et al*., 2006).

Currently, MTT estimations are mainly based on two assumptions, the steady-state assumption (SSA) and the non-steady-state assumption (NSSA), with each corresponding to specific ecological principles and applicable conditions. Without changes in external driving forces, such as disturbances and climate change, the internal processes of an ecosystem will gradually drive the ecosystem C cycle toward equilibrium (Luo and Weng, 2011), at which C

74 influx equals efflux, C pools are stabilized and the long-term net ecosystem C exchange
75 becomes zero (i.e., $\overline{\Delta C} = 0$); therefore, the MTT under the SSA can be defined as
76 "stock/influx" (Rodhe, 1978). When ecosystems are subject to natural (e.g., insect outbreaks
77 and fire) and anthropogenic (e.g., land-use change) disturbances as well as global changes
78 (e.g., increasing atmospheric CO_2, climate warming, and nitrogen deposition), ecosystem C
79 cycling processes become destabilized (Luo and Weng, 2011; Bellassen *et al*., 2011).
80 Therefore, C pools in ecosystems vary dynamically over time (i.e., $dC/dt \neq 0$), the C influx is
81 not equal to the C efflux, and the MTT under the NSSA should be defined as "stock/efflux"
82 (Schwartz, 1979).

83 An exact equilibrium is almost impossible to observe in reality; but when the relative
84 difference between input and output is negligible, it is justified and valid to apply SSA (Odum,
85 1969), usually occurring at large or coarse spatial scales where sufficient variation in the
86 sink/source distribution could balance the gross influx and efflux, or occurring at long-time
87 scales where the effects of transient changes in climate or atmospheric CO_2 could be ignored.
88 Specifically, at the global or continental scale near steady state, the more readily obtained
89 influx can be used to estimate MTT instead of the efflux (Carvalhais *et al*., 2014; Yan *et al*.,
90 2014). In addition, key process parameters, such as the allocation and turnover rates, can be
91 optimized and then incorporated into an analytical expression under the SSA to quantify the
92 spatial patterns of ecosystem MTT (e.g., Barrett, 2002; Xia *et al*., 2013). Furthermore, the
93 state of C pools in global models can be initialized via the spin-up process by iterating from
94 hundred to thousand years in preindustrial period until equilibrium (Taylor *et al*., 2012),
95 which determines the C pool size used in the analysis of MTT (Todd-Brown *et al*., 2013;
96 Exbrayat *et al*., 2014; Koven *et al*., 2015).

97 In addition to these aforementioned applications, the SSA has also been widely invoked
98 in MTT research over a considerable range of temporal and spatial scales (e.g., Zhou & Luo,

2008; Galbraith *et al*., 2013; Thurner *et al*., 2016; Wang *et al*., 2018), over which non-steady behaviour may exist. This appears to be an imperative choice in the absence of direct measurement of C effluxes, such as heterotrophic respiration, or current or past-historical ecosystem states for constraining the dynamic ecosystem C cycle processes. Specifically, at the regional scale with considerable C sinks, (1) the MTTs are still obtained based on influx, which is much higher than efflux, e.g., in the forest ecosystems in eastern China (Wang *et al*., 2018) and the tropics (Galbraith *et al*., 2013) that have been shown to be major C sinks globally (Piao *et al*., 2009; Pan *et al*., 2011; Yu *et al*., 2014); (2) C turnover rates and allocation coefficients are still retrieved under the SSA but further used in a transient simulation of the regional MTT and net ecosystem productivity (NEP) (Zhou & Luo., 2008; Zhou *et al*., 2010, 2013b); (3) As global C models have been developed to fine spatial scales, the SSA is also widely used for C pool state initialization at local scales with dynamic C sources or sinks (e.g., young-aged forests) (Law *et al*., 2001; Morales *et al*., 2005; Carvalhais *et al*., 2008, 2010; Huang *et al*., 2011). Previous studies have reported the uncertainty in C pool states and C cycle parameters induced by the SSA (e.g., Carvalhais *et al*., 2008, 2010), which may further affect the validity of MTT estimation via the "stock/flux" approach. Therefore, a better understanding of the mismatch between the ideal SSA and realistic disequilibrium state in C turnover time estimation is needed and the effect of such inconsistencies on C sequestration should be determined.

With the development of observational technology and the accumulation of multiple and time-series C cycle datasets over the past decade, our understanding of terrestrial C dynamics has improved; accordingly, C effluxes can be better constrained to return to the definition of MTT at the realistic disequilibrium state (e.g., Bloom *et al*., 2016). On this basis, researchers have attempted to develop the model-data fusion (MDF) method to estimate ecosystem MTT under the NSSA, which integrates the process-based model and observational data to estimate

these C cycle dynamics in better agreement with the actual disequilibrium state (Luo *et al*., 2003; Xu *et al*., 2006; Zhang *et al*., 2010; Zhou *et al*., 2013b; Bloom *et al*., 2016). Moreover, the uncertainty in allocation and turnover parameters as well as C pool states have largely been reduced based on the time-series observations under the NSSA, thereby significantly enhancing the model's ability to predict MTT and NEP (Safta *et al*., 2015; Smallman *et al*., 2017).

Regardless, a detailed comparative analysis of ecosystem MTT estimations under the NSSA and SSA has not been conducted based on multi-source and long-term continuous observational data. In this study, we systematically examined differences in ecosystem C cycle states and processes estimated under the two assumptions as well as the underlying mechanisms within a robust analytical framework, using large amounts of long-term continuous observational soil, biology, and climate data for 10 typical forest ecosystems from the Chinese Ecosystem Research Network (CERN) that represent the East Asian monsoon region, a large C sink accounting for 8% of the global forest NEP (Yu *et al*., 2014). Our analysis mainly focuses on the mismatch between the two assumptions with regard to (1) the magnitude and spatial pattern of the ecosystem MTT, (2) the relationship between the ecosystem MTT and climate, and (3) the ecosystem C sink in these forest ecosystems. These quantitative comparisons using the proposed framework could provide a reference for future MTT research in terms of SSA/NSSA method selection and facilitate an awareness of the corresponding uncertainty.

Materials and Methods

2.1 Site description

The eastern China monsoon region covers tropical, subtropical, warm temperate, and temperate climate zones from south to north, and subhumid and humid areas from north-west

to south-east. The large precipitation and temperature gradients support diverse forest ecosystems ranging from evergreen broad-leaved and coniferous forests to deciduous coniferous and broad-leaved forests. Here we selected 10 permanent plots with long-term observational data from CERN to cover the typical forest types with various ages in this region (Fig. 1; Table S1). All 10 sites are well protected and subject to minimal disturbance.

2.2 Data

The collected data are divided into four meteorological driving data, five stock-related constraint datasets of soil, foliage, root, wood, and leaf area index (LAI), and three flux-related constraint datasets of litterfall, net ecosystem exchange (NEE) and soil respiration (Rs). The time-series observations at most of the sites cover the period from 2005 to 2015, but those of SNF, which was incorporated into CERN later, are from 2010 to 2015 (Table S2).

2.2.1 Biometric data

At each site, the biomass of leaves, branches, stems, and roots were estimated from the measured diameters at breast height (DBHs) and tree heights using the allometric method. The biomass inventory was performed at least once every five years. To split fine and coarse root biomass, the ratio of the fine root biomass to the entire root biomass in typical Chinese forests was obtained from Zhang *et al*. (2001), and the coarse root biomass was then combined with the branch and stem biomasses to constitute the woody biomass. Estimates of leaf, fine root, and woody biomass were used to constrain the corresponding C pools in the inverse analysis.

The aboveground litterfall biomass was measured by 10 replicates of 100 cm × 100 cm baskets monthly during the growing season or once during the non-growing season. All collected litter was dried at 70 °C for 24 h and weighed. We used annual litterfall biomass

data for the inverse analysis to avoid the effect of wind on the measurement of litterfall biomass within an individual month.

The LAI at each site was measured optically with a LAI-2000 plant canopy analyser (LI-COR, Lincoln, NE, USA) at least quarterly every year and corrected by the foliage clumping index, which was set for plant functional type (PFT)-specific empirical values as reported in Zhu *et al.* (2012). The seasonal variation in the LAI combined with the leaf C mass per leaf area (LCMA) parameter constrained the dynamic trajectory of the leaf C pool in the MDF analysis.

2.2.2 Soil data

Soil C content was calculated from soil organic matter (SOM) measured by the potassium dichromate oxidation titrimetric method and soil bulk density measured by the cutting ring method in each field campaign at 10 forest sites. At least three samples were collected from each of five soil layers (0–10, 10–20, 20–40, 40–60, and 60–100 cm) once every five years. We calculated the soil organic C (SOC) as follows (Post *et al*., 1985; Eqn. 1).

$$SOC = \sum_{i=1}^{n} 0.58 \times H_i \times B_i \times O_i \times 100 \quad (1)$$

where SOC is soil organic C density (g C/m^2) of all n layers, H_i is soil thickness (cm), B_i is soil bulk density (g/cm^3), and O_i is SOM content of the i_{th} layer (%).

2.2.3 Flux data

NEE data were obtained from ChinaFLUX, covering CBF, QYF, ALF, and BNF. The data were aggregated to the daily time step from half-hourly CO_2 flux data measured by the eddy covariance technique and processed by quality control and gap filling (Li *et al*., 2008). To reduce the impact of gap-filled data on parameter estimations, we only aggregated NEE

data for the days with at least 50% observed half-hourly fluxes, which were relatively evenly distributed in the daytime and nighttime.

Rs data were measured using static chamber-gas chromatography techniques at CBF, QYF, DHF, HSF, and BNF (Zheng, 2010). A total of 4–6 replicates were measured 2–3 times per month with sampling times between 9:00 am and 11:00 am. In this study, the monthly averaged heterotrophic respiration (Rh) was obtained according to the ratio of root respiration to Rs in the typical Chinese forest ecosystem to constrain the seasonal variation of C efflux from litter and soil in the inverse analysis (Chen *et al*., 2008).

2.2.4 Meteorological data

In situ observations of daily air temperature (T), photosynthetically active radiation (PAR), relative humidity (RH), and saturated vapour pressure difference (VPD) at the 10 sites from 2005 to 2015 were obtained from the CERN scientific and technological resources service system (http://www.cnern.org.cn/) and processed by standardized quality control and gap filling (Li *et al*., 2008; Liu *et al*., 2017a).

2.3 Model

Data Assimilation Linked Ecosystem Carbon (DALEC) has been applied extensively in the MDF framework (Richardson *et al*., 2010; Bloom *et al*., 2016). It is a box model of C pools connected via fluxes running at a daily time step, and its main structure (i.e., C cycle, C allocation, and turnover process) is generally consistent with the state-of-the-art process-based models (Fig. 2). Here, we used two versions of DALEC, an evergreen forest-specific version (DALEC-E; Williams et al 2005) with five pools (i.e., foliage, fine root, woody (including branch, stem, and coarse root), litter and SOM) and a deciduous forest-specific version (DALEC-D; Fox et al., 2009) with an additional labile pool of stored C that supports leaf flushing.

The detailed C cycle of forest ecosystems can be characterized by several properties (Xia *et al*., 2013): (1) the C cycle is usually initiated with the canopy C influx GPP. Specifically, GPP is estimated herein using a canopy photosynthesis model (Ji, 1995; Appendix S1), which is a function of LAI, PAR, T, and RH. Note that the daily LAI is estimated as the ratio of the simulated foliar C pool and optimized LCMA parameter. (2) GPP is consumed in a certain fraction (f_{auto}) as autotrophic respiration (Ra) and partitioned into various plant pools (i.e., foliar, labile, wood, and fine roots); then, the degraded C from biomass pools goes to two dead organic matter pools with temperature-dependent losses (Rh). (3) C transfers are dominated by the donor pools (e.g., the litter decomposing into soil). (4) C exiting from C reservoirs is based on the first order differential equation. These properties of the forest C cycle in DALEC can be mathematically described by a matrix model as Eqn. 2 and determined as a function of key C cycle parameters (Table S3). All these parameters will be optimized based on the stock- and flux-related observations.

$$\frac{d\mathbf{C}}{d\mathbf{t}} = BI(t) - A\xi kC(t) \quad (2)$$

where C(t) is a vector of C pool sizes at time t; $B = (f_{fol} \quad f_{roo} \quad f_{woo} \quad 0 \quad 0)^T$represents the partitioning fractions from photosynthetically fixed C input to the foliage (f_{fol}), root (f_{roo}), woody (f_{woo}), litter, and soil pools; $I(t)$ is the input flux of fixed C via plant photosynthesis; $k = diag(\theta_{fol}, \quad \theta_{roo}, \quad \theta_{woo}, \quad \theta_{min} + \theta_{lit}, \quad \theta_{som})$, a diagonal matrix of exit rates to quantify the fraction of C left from the foliage (θ_{fol}), root (θ_{roo}), woody (θ_{woo}), soil (θ_{som}), litter (θ_{lit}) pool, and the litter mineralization rate into soil (θ_{min}); and $\xi = diag(1, \quad 1, \quad 1, \quad f(T), \quad f(T))$, a diagonal matrix of temperature scalar $f(T)$ to quantify response of C decay rate to changes in temperature. The response to soil moisture was not considered in DALEC given the overall good moisture condition in these forest ecosystems (MAP=1160.18±413.79 mm). A is a square matrix of transfer coefficients to quantify C movement among pools as follows:

242 $$A = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ -1 & -1 & 0 & 1 & 0 \\ 0 & 0 & -1 & -\frac{\theta_{min}}{\theta_{min}+\theta_{lit}} & 1 \end{pmatrix}$$

243 **2.4 Estimation of ecosystem MTT and NEP based on the MDF framework**

244 The analytical framework developed here systematically considered the C pool initial
245 state, cost function, observational and forcing data involved in the inverse analysis, and
246 formula for estimating MTT to diagnose the SSA-induced bias in contrast to the NSSA,
247 which affected parameter retrieval and the estimation of MTT and NEP (Fig. 3). Note that
248 models were the same in the NSSA and SSA setups. The temporal domains for model
249 simulation were from 2005 to 2015.

250 2.4.1 Parameter estimation under the SSA and NSSA

251 Under the NSSA, C pools are time-variant, i.e., C influx is not equal to the C efflux, thus
252 not restricted to NEP ~0; the dynamic long-term observations of C stocks and fluxes were
253 used to constrain the DALEC model. As an important factor that may affect the estimated
254 MTT and NEP, the initial state of the C pools was determined by the initial observation of C
255 stocks or optimized (i.e., the labile pool, which cannot be directly observed) to avoid the
256 uncertainty arising from the spin-up process. Then, the turnover and allocation parameters
257 were inverted under the disequilibrium state (Eqn. 3) with dynamic environmental forcing.

258 $$\begin{cases} \frac{dC}{dt} \neq 0 \\ C_i(\mathrm{t}+1) = C_i(\mathrm{t}) + I_i(\mathrm{t}) - k_i C_i(\mathrm{t}), \mathrm{i} = 1,2 \ldots \mathrm{n} \\ C_i(\mathrm{t}=0) = C_i 0 \end{cases} \quad (3)$$

259 where C_i, I_i, k_i represent the size, input and turnover rate of the i_{th} C reservoir, respectively;
260 C_i0 represent the initial state of the i_{th} C reservoir; and t represent the daily step. According to

the Bayesian theory, the posterior distributions of parameters are calculated by maximizing the likelihood function (Eqn. 4).

$$L_{NSSA} = \prod_{j=1}^{m} \prod_{i=1}^{n_j} \frac{1}{\sqrt{2\pi}\sigma_j} e^{-\left(x_{j,i} - \mu_{j,i}(\boldsymbol{P_{NSSA}})\right)^2 / 2{\sigma_j}^2}, \ m = 1,2,\dots 8 \quad (4)$$

where L_{NSSA} is the integrated likelihood function under the NSSA; m is the number of multiple data types; n is the number of data points in the j_{th} data type; $x_{\mathrm{j,i}}$ is the measured value composed of eight dynamic C stock and flux observations; $\mu_{\mathrm{j,i}}(p_{\mathrm{NSSA}})$ represents the modeled fluxes and stocks based on parameters under the NSSA (P_{NSSA}); and σ_{j} is the standard deviation of each data point in the j_{th} data type.

Under the SSA, C pools are stabilized such that an additional constraint of long-term NEP ~ 0 was used to constrain the initial state of C pools at steady state, in addition to the observed C stock and flux constraints. As the meteorological forcing spans 2005 to 2015, we averaged total ecosystem C pools ($\mathrm{C_{TOT}}$) over each 10-year segment to obtain $\overline{\mathrm{C_{TOT}}}$, and determined steady-state criterion by which changes in $\Delta\overline{C_{\mathrm{TOT}}}$ (Eqn. 6) between two neighbouring segments are within a threshold of 0.5 g C m^{-2} yr^{-1} (as one criterion in Thornton and Rosenbloom, 2005 and Xia *et al*., 2012).

$$\Delta\overline{C_{\mathrm{TOT}}} = \left|\overline{C_{\mathrm{TOT}}(\mathrm{t}+1)} - \overline{C_{\mathrm{TOT}}(\mathrm{t})}\right| \leq 0.5 \quad (5)$$

where t represents the period for parameter optimization during 2005 to 2015.

The C turnover and allocation parameters were retrieved under the repeated 10 year (2005–2015) cycle of meteorological forcing until the initial state of C pools were stationary at the annual time scales (i.e., long term NEP ~ 0, Eqn. 5), and the likelihood function was maximized compared to the observations (Eqn. 6).

$$L_{SSA} = \prod_{j=1}^{m} \prod_{i=1}^{n_j} \frac{1}{\sqrt{2\pi}\sigma_j} e^{-\left(x_{j,i} - \mu_{j,i}(\boldsymbol{P_{SSA}})\right)^2 / 2{\sigma_j}^2}, \ m = 1,2,\dots 8 \quad (6)$$

where $\mu_{j,i}(P_{SSA})$ represents the modelled values based on parameters under the SSA (P_{SSA}), and L_{SSA} is the integrated likelihood under the SSA and consists of five stock-related observations, two efflux observations (litterfall and Rs), and the tolerance of long-term NEE described in Eqn. 5.

Specifically, we applied the Metropolis simulated annealing algorithm, a variation of the Markov Chain Monte Carlo (MCMC) technique, for parameter estimation (Zobitz *et al*., 2011). Besides, ecological and dynamic constraints were imposed on the DALEC parameters and pool dynamics (Appendix S2) which can significantly reduce uncertainty in model parameters and simulations (Bloom and Williams, 2015).

2.4.2 Estimation of ecosystem MTT under the SSA and NSSA

Here, we use the MTT_(MDF scheme, i.e., SSA/NSSA)_(flux term used, i.e., Input (I) /Output (O)) to consistently define the C turnover times in different analyses. Under the SSA, long-term NEP = 0; i.e., the C influx equalizes the efflux, such that the ecosystem MTT can be defined as the ratio of retrieved total ecosystem C stocks to the ecosystem influx (Sanderman *et al*., 2003, Eqn. 7).:

$$MTT\_SSA\_I = \frac{\overline{C_{pool\_SSA}}}{\overline{I_{SSA}} - \Delta\overline{C_{pool}}} = \frac{\overline{C_{pool\_SSA}}}{\overline{I_{SSA}}} \quad (7)$$

where *MTT_SSA_I* is the ecosystem MTT under the SSA as estimated from C influx, $\overline{C_{pool\_SSA}}$ is the mean annual ecosystem C pool, $\overline{I_{SSA}}$ is the mean annual ecosystem C input (GPP), and $\Delta\overline{C_{pool}}$ is the change in the ecosystem C pool.

We have further derived an analytical expression for MTT_SSA_I (Eqn. 8):

$$MTT\_SSA\_I = \frac{\sum_i^n \overline{C_{pool_i\_SSA}}}{\overline{I_{SSA}}} = \frac{\overline{I_{i\_SSA}}}{\overline{I_{SSA}}} \times \frac{\sum_i^n \overline{C_{pool_i\_SSA}}}{\overline{I_{i\_SSA}}} \quad (8)$$

$$= \left(\frac{f_{fol}}{\theta_{fol}} + \frac{f_{roo}}{\theta_{roo}} + \frac{f_{woo}}{\theta_{woo}} + \frac{f_{fol}+f_{roo}}{(\theta_{min}+\theta_{lit})\times\xi} + \frac{f_{woo}+(f_{fol}+f_{roo})\times\frac{\theta_{min}}{\theta_{min}+\theta_{lit}}}{\theta_{som}\times\xi} \right) \times (1 - f_{auto})$$

$$= (1\ 1\ \ldots\ 1)(\mathrm{A}\xi k)^{-1} B(1 - f_{auto})$$

where $\overline{C_{pool_{\iota\_SSA}}}$ and $\overline{I_{\iota\_SSA}}$ represent the mean annual size and influx of the i_{th} C pool, respectively, which are simulated based on the site-specific SSA-optimized parameters at each site.

This form is compatible with the inverse matrix composed of the optimized allocation, turnover, and transit parameters (Xia *et al*., 2013; Luo *et al*., 2017), which consider the ecosystem MTT to be aggregated from the sum of turnover times for pools in series and the influx-weighted turnover time of pools in parallel (Barrett, 2002). The inherent consistency is theoretically supported by Sierra *et al*. (2017), because both forms are based on the hypothesis that the size of the C pool is equivalent to the product of C input flux and C turnover time in the equilibrium state (Bolin and Rodhe, 1973).

Under the NSSA, each C pool is an instantaneous state variable; thus, the efflux-weighted turnover time of pools is also time-varable and cannot be parameterized. Therefore, constructing an inverse matrix explicitly composed of the turnover and allocation parameters to represent the MTT is difficult. In this case, the ratio of the total ecosystem C stock to the efflux simulated based on these optimized parameters under NSSA is used to estimate ecosystem MTT (Schwartz, 1979; Bloom *et al*., 2016; Eqn. 9).

$$MTT\_NSSA\_O = \frac{\overline{C_{pool\_NSSA}}}{\overline{I_{NSSA}} - \Delta C_{pool}} = \frac{\overline{C_{pool\_NSSA}}}{\overline{O_{NSSA}}} \quad (9)$$

$$= \frac{\sum_i^n \overline{C_{pool_{\iota\_NSSA}}}}{\overline{O_{NSSA}}} = \frac{\overline{O_{\iota\_NSSA}}}{\overline{O_{NSSA}}} \times \frac{\sum_i^n \overline{C_{pool_{\iota\_NSSA}}}}{\overline{O_{\iota\_NSSA}}}$$

$$= (1\ 1\ \ldots\ 1)(\xi k)^{-1} w$$

where $w = \left(\frac{\overline{O_{fol\_NSSA}}}{\overline{O_{NSSA}}}, \frac{\overline{O_{woo\_NSSA}}}{\overline{O_{NSSA}}}, \frac{\overline{O_{roo\_NSSA}}}{\overline{O_{NSSA}}}, \frac{\overline{O_{lit\_NSSA}}}{\overline{O_{NSSA}}}, \frac{\overline{O_{som\_NSSA}}}{\overline{O_{NSSA}}}\right)$;

MTT_NSSA_O is the ecosystem MTT under the NSSA based on C output; $\overline{C_{pool\_NSSA}}$ is the mean annual ecosystem C pool; $\overline{I_{NSSA}}$ is the mean annual ecosystem C input (GPP); $\overline{O_{NSSA}}$ is the mean annual ecosystem C output (RE); $\overline{C_{pool_{i}\_NSSA}}$ and $\overline{O_{i\_NSSA}}$ represent the mean annual size and output of the i_{th} C pool, respectively; *w* represents the output-dependent weight of C pools; and $\overline{O_{fol\_NSSA}}$, $\overline{O_{woo\_NSSA}}$, $\overline{O_{roo\_NSSA}}$, $\overline{O_{lit\_NSSA}}$, and $\overline{O_{som\_NSSA}}$ represent the mean annual output of the foliage, wood, root, litter and soil pools, respectively. All C stocks and fluxes were simulated based on the site-specific NSSA-optimized parameters at each site. Because the C reservoirs, fluxes, and turnover times are instantaneous values, we used the average of the fluxes and reservoirs for multiple years to reflect the average turnover time during a specific period (i.e., 2005-2015). Note that with few natural and anthropogenic disturbances at these well-protected CERN sites (Zhou *et al*., 2006; Zhang *et al*., 2010), the total ecosystem output was approximately equivalent to the RE.

2.4.3 Estimation of ecosystem NEP based on the SSA- and NSSA-inverted parameters

The optimized parameter values under the NSSA and SSA along with the initial observations of corresponding C pool sizes were used in forward modeling driven by the dynamic environmental variables from 2005 to 2015 (Zhou *et al*., 2008). NEP was further derived from the difference between the ecosystem C influx and RE to examine the effects of retrieved parameters on C sequestration under different hypotheses.

2.5 Estimation of ecosystem MTT based on observation

To test the robustness of MTT_SSA_I based on SSA-inversion at the 10 sites, the MTT under the SSA based on observed influx (MTT_OBS_I) was calculated from the ratio of mean annual total ecosystem stock measurements in CERN and the mean annual GPP observed

from moderate resolution imaging spectroradiometer (MODIS) (Carvalhais *et al*., 2014). MODIS products of GPP (MOD17A2H, 500m) at each site were downloaded from the University of Oklahoma Data Center (http://www.eomf.ou.edu/visualization/manual/) and then accumulated to the annual time step from the 8-day observational data. Because the annual MODIS GPP values are consistent with the tower-based GPP at the flux sites (Fig. S1, $R^2 = 0.90$, $p < 0.01$, mean absolute error (MAE) = 37.39 g C m^{-2} yr^{-1}), it is reasonable to use this high-resolution product as a reliable observation at the site scale.

Results

3.1 Key parameters retrieved under the SSA and NSSA

Under the NSSA, the ratio of Ra to GPP (f_{auto}) varied from 0.3 to 0.7, with a mean value of 0.53, showing a trend of first decreasing and then increasing with decreasing latitude (Figs. 4a and S2). The proportion of NPP allocated to wood (f_{woo}) ranged from 0.5 to 0.9, with a mean value of 0.67, showing an increasing trend with decreasing latitude (Figs. 4d and S2). The MTTs (i.e., the inverse of the turnover rate) of wood, soil, foliage, fine root, and litter at the 10 sites were 48.54, 86.55, 3.12, 2.40, and 1.13 years, respectively. Specifically, the turnover rate of wood and soil (θ_{woo} and θ_{som}), the two largest C pools in living vegetation and dead organic matter, respectively, showed obvious increasing trends with decreasing latitude (Figs. 4g, 4i, and S2). The temperature sensitivity of soil decomposition (Rh_{temp}) exhibited a spatial pattern of tropical forest > temperate forest > subtropical forest (Figs. 4k, and S2). However, compared to the key C-cycle parameters under the NSSA, the allocation to faster-turnover C pools under the SSA was mostly overestimated ($f_{auto,}f_{fol}$), but to slow-turnover pools (f_{woo}) was underestimated; turnover rate of major pools (θ_{woo} and θ_{som}) were overestimated; furthermore, the sensitivity to

climate (Rh_{temp}) was underestimated; and these parameters lacked obvious spatial patterns (Figs. 4a, 4c, 4d, 4g, 4i, and 4k).

We compared the modelled and observed datasets to validate the inverted parameters based on multi-source data. Under the NSSA, the simulated and observed vegetation and soil C stocks and C fluxes agreed well, with the scatter points falling along the 1:1 line (Fig. 5). Specifically, the determination coefficients (R^2) for C stocks varied between 0.94 and 0.99, and the root-mean-square errors (RMSEs) were small relative to their magnitudes (Fig. 5a-e). In contrast, R^2 for C fluxes (NEE and Rs) were slightly lower (0.45–0.50), but the RMSEs were only 1.37 and 0.67 g C m^{-2} d^{-1}, respectively (Fig. 5 g, h). Under the SSA, the model performance regarding the C stocks was comparable with that under the NSSA (Fig. 5a-e), but due to the overestimation of C turnover rates (Fig. 4e-j), simulated C effluxes, such as litterfall and Rs, were markedly overestimated, which in turn overestimated NEE (Fig. 5f-h).

3.2 Magnitude of MTT and its relationship with forest age under the SSA and NSSA

At the 10 sites, the MDF-based ecosystem MTT under NSSA (MTT_NSSA_O) and SSA (MTT_SSA_I) and the observation-based ecosystem MTT under SSA (MTT_OBS_I) ranged from 9.64 to 38.23, 7.29 to 33.59, and 8.73 to 36.31 years, with averages of 24.44, 17.27, and 17.20 years, respectively. As MTT_SSA_I and MTT_OBS_I were nearly identical (Fig. 6b, MAE = 0.25, $R^2 = 0.86$, $p < 0.001$), MTT_SSA_I was selected to represent the estimated MTT under SSA in the ensuing analyses.

The ecosystem MTT_SSA_I was significantly lower (with an average of 29%) than the MTT_NSSA_O (Fig. 6a, $p < 0.05$). Because wood and soil are the two largest C pools in forest ecosystems, the differences in their turnover rates estimated under the SSA and NSSA and the relative contributions to the difference between the whole-ecosystem MTT_SSA_I and MTT_NSSA_O (ΔMTT) deserved further analysis. Both the θ_{woo} and θ_{som} were

significantly overestimated under the SSA (Figs. 4g, 4i) with the magnitude of the overestimation for θ_{woo} being greater than that for θ_{som} (1.24E-04 vs 5.02E-05), which largely accounted for the ecosystem ΔMTT. Meanwhile, less C was allocated to slow-turnover structural C pools under the SSA (Fig. 4d, $f_{\text{woo\_SSA}} = 0.46$ vs $f_{\text{woo\_NSSA}} = 0.68$), thus leading to underestimations of the vegetation MTT and ecosystem MTT.

The ecosystem ΔMTT varied among different ecosystems (Fig. 6a), and these differences should be closely associated with how far the ecosystems deviate from the equilibrium state, as most likely reflected by the age-related growth. Thus, forest age was used as a proxy of the gap between the actual and equilibrium state. We found that the forest age accounted for more than 50% of the variation in ecosystem ΔMTT with a significantly negative correlation (Fig. 7a, $p < 0.005$). Further analysis revealed that rather than the overestimation of θ_{som}, the overestimation of θ_{woo} under the SSA ($\Delta\theta_{woo}$), which exhibited a significant power function relationship with forest age, dominated the age-dependent ΔMTT in the entire ecosystem (Figs. 7b, S3).

3.3 Latitudinal pattern of MTT and its covariance with climate under the SSA and NSSA

The ecosystem MTT_NSSA_O and MTT_SSA_I exhibited similar latitudinal patterns, both of which decreased with decreasing latitude (Fig. 8a), showing a pattern of temperate MTT > subtropical MTT > tropical MTT (Fig. 6a). ALF appears to be an outlier, mainly due to its high elevation (2488 m) and special vertical zonality. We further analysed the relationship between MTT and climate, which is recognized as an important factor regulating the latitudinal MTT gradient (Carvalhais *et al*., 2014). Both the ecosystem MTT_SSA_I and MTT_NSSA_O were negatively correlated with temperature and precipitation (Figs. 8b, 8c), but the sensitivity of the MTT_SSA_I to these two climatic variables was significantly lower

than that of the MTT_NSSA_O, which decreased from 1.02 yr/°C to 0.80 yr/°C (by 22%) for temperature and from 1.34 yr/100 mm to 0.78 yr/100 mm (by 42%) for precipitation.

3.4 Ecosystem C sequestration based on the SSA- and NSSA-inverted parameters

Under the dynamic environmental conditions, all 10 forests were net C sinks based on both the SSA- and NSSA-inverted parameters (Fig. 9). However, with respect to actual eddy covariance observations, the NEP was obviously underestimated with the SSA-inverted parameters, whereas the NEP based on NSSA parameters was highly consistent (Fig. 5g); for example, the mean annual NSSA-estimated and observed NEP were 347.4 and 306.6 g C m^{-2} yr^{-1} at CBF, respectively, and 465.9 and 469.3 g C m^{-2} yr^{-1} at QYF. Overall, the mean annual NEP for 10 typical forest ecosystems in eastern China monsoon region reached 325.2 g C m^{-2} yr^{-1} based on NSSA-inverted parameters, which was 4.83 times that estimated with SSA-inverted parameters (67.3 g C m^{-2} yr^{-1}). Furthermore, the SSA-induced bias in NEP was significantly greater ($p < 0.05$) in young and middle-aged forests (7.3-fold) than that in mature forests (3.8-fold). The underestimation of NEP in SSA analysis was largely due to the overestimation of RE, which is closely associated with the overestimation of C turnover rates and allocations to fast-turnover pools (Fig. 4); whereas GPP was comparable to that under the NSSA (Fig. S4).

Discussion

4.1 Robustness of MTT estimations under SSA and NSSA

The robustness of MTT_SSA_I estimations in the 10 ecosystems has been assessed with respect to MTT_OBS_I, which is generally recognized as a benchmark in current research (e.g., Thurner *et al*., 2017). Although eddy covariance measurements for MTT_OBS_I estimation are lacking for some of the sites, the MOD17A2H product performed as a suitable alternative for GPP observations because its spatial resolution is finer that the footprint of the

flux towers (Mi *et al*., 2006; Zhao *et al*., 2005). Furthermore, we found the magnitude and spatial pattern of ecosystem MTT_SSA_I in eastern China monsoon forests were consistent with various MTT_SSA estimations by observation or inversion approach in regional or global forest ecosystems (Table S4). A negative correlation of MTT_SSA_I with both temperature and precipitation was observed in this study, which was supported by research on MTT_SSA_I based on forest inventory and remote sensing observations (Gill and Jackson, 2000; Sanderman *et al*., 2003; Carvalhais *et al*., 2014). The high consistency and robustness of MTT_SSA calculated by various methods indicated that the deviation in MTT_SSA identified in this study has broad implications for various SSA applications in C cycle research.

Due to the complexity of ecosystem C emission processes and the scarcity of ecosystem efflux data, it remains challenging to validate the inverted MTT_NSSA_O of whole-ecosystem with respect to observation-based estimates at disequilibrium state. However, the magnitude of the key process parameters regulating the ecosystem MTT under the NSSA as inferred in this study was broadly consistent with a number of empirical studies on C allocations, vegetation turnover rates and mortality, and soil decomposition rates (Table S5). The turnover times of fine roots measured from $\delta^{13}C$ signals tend to be systematically overestimated due to sampling biases, with the finest and most ephemeral roots being missed (Strand *et al*., 2008). Regarding the pattern of these key processes, f_{auto} first decreased and then increased as temperature increased at the turning point of approximately 11°C, which was highly congruent with the synthetic analysis based on the global forest database and could be ascribed to the asymmetric response of RE and GPP to rising temperature (Piao *et al*., 2010). The decrease in f_{woo} with increasing latitude and decreasing temperature was supported by the inventory-based synthesis in Chinese forests (Li *et al*., 2009), and this pattern may be explained by the adaptive strategies of forest trees to temperature (Reich *et al*., 2014) as well

as the age-structure-related strategy (Zhou *et al*., 2013b), which tends to allocate less C to the structural pool in old forests mainly distributed in cold, high-latitude regions in China (Zhang *et al*., 2014). θ_{woo} and θ_{som} both increased with rising temperature, which agrees well with the variation in the plant mortality rate based on forest inventory (Mantgem *et al*., 2009; Zhou *et al*., 2013a) and the variation in soil C decomposition based on Rs observations from the chamber or isotope method (Karhu *et al*., 2010; Frank *et al*., 2012; Chen *et al*., 2013). In addition, Rh_{temp} was higher in tropical and temperate forests than subtropical forests, which is consistent with the regional variation in temperature sensitivity in Chinese forests based on field sampling and incubation experiments (Liu *et al*., 2017b; Zhou *et al*., 2009).

Overall, the robustness of estimations under the NSSA compared to the empirical research indicates that the C cycle dynamics estimated by NSSA method match the realistic observations well. Thus, the SSA-induced bias in MTT estimation and the underlying mechanism can be reliably quantified in contrast to our estimations under NSSA.

4.2 Identification of the uncertainty in MTT under SSA

Under the background of global environmental changes, extensively distributed disturbances drive the ecosystems far from a steady state at local scales (Luo and Weng, 2011), which makes the spatially-specific research a great challenge. Although the spatial aggregation of regional/global may approximately estimate the MTT under the SSA (Odum, 1969), identifying the explanatory mechanism is difficult because the aggregation also merges some spatially heterogeneous influencing factors, such as temperature and terrain, that nonlinearly impact the MTT. In addition, previous studies have challenged the inherent concept behind SSA for the ecosystem C cycle (Lugo & Brown, 1986; Cannell & Thornley, 2003), e.g., whether SSA-applicable old-growth forests are quasi-neutral or large C sinks (Zhou *et al*., 2006; Luyssaert *et al*., 2008). Moreover, some uncertainties from the SSA have been revealed in C cycle studies; e.g., model initialization until equilibrium systematically

493 overestimated the C pools (Pietsch & Hasenauer, 2006), exhibiting a 6-fold range among
494 various global C models (Exbrayat *et al*., 2014). This further led to compensatory biases in
495 NEP simulation, whereas relaxing the SSA in initialization made a 92% decrease in NEP
496 errors (Carvalhais *et al*., 2008, 2010). Besides, key turnover parameters determined under the
497 SSA were overestimated, e.g., the decay rate of recalcitrant pools (Wutzler & Reichstein,
498 2007); this further resulted in underestimation of NEP in transient simulation, which may be
499 up to 30% even when C sinks only account for 10% of the C input in disequilibrium
500 ecosystems (Zhou *et al*., 2013b). It is noteworthy that these biases in pool initialization and
501 parameter inversion will propagate into the MTT estimation via the "pool/flux" method and
502 need to be determined.

503 Our study provides a new MDF framework to trace the uncertainty in turnover time
504 induced by traditional SSA through direct comparison with the realistic disequilibrium state
505 rather than conducting sensitivity experiments as reported in Carvalhais *et al*. (2008) or Zhou
506 *et al*. (2014). Additionally, we collectively consider the factors resulting in the mismatch
507 between MTT_SSA_I and MTT_NSSA_O, i.e., the pool initialization, the turnover and
508 allocation parameter inversions as well as the formulas for estimating MTT used under two
509 assumptions (Fig. 3). Via this framework, a significant underestimation in MTT_SSA_I was
510 observed in these sites, which may be partly explained by the overestimated turnover rates and
511 underestimated allocation to structural pools under SSA (Fig. 4). Moreover, in ecosystems
512 with substantial sinks where GPP is much higher than RE, the input-based MTT_SSA_I
513 should be smaller than the output-based MTT_NSSA_O, which might be more evident in
514 younger forests due to the intrinsic relationship between age and forest growth (Zaehle *et al*.,
515 2006; Goulden *et al*., 2011).

516 To further distinguish the SSA-induced biases arising from the parameterization or the
517 MTT estimation, we contrasted MTT_NSSA_O vs MTT_SSA_O (R^2 = 0.76, RMSE = 9.01 yr)

and MTT_NSSA_I vs MTT_SSA_I (R^2 = 0.74, RMSE = 4.41 yr) to obtain the biases that only stem from the improper use of SSA in parameterization. We found that these biases were much higher than those induced by only using SSA in MTT estimation, i.e., MTT_NSSA_I vs MTT_NSSA_O, or MTT_SSA_I vs MTT_SSA_O (Table S6). This indicated that the effect of the improper SSA on parameterization was deeper than that on MTT estimation, which provides a significant caveat for SSA applied especially in model optimization (e.g., Barret *et al*., 2002; Zhou & Luo, 2008; Zhou *et al*., 2010, 2013b). In the future, with the accumulation of spatiotemporal observations (Le Toan *et al*., 2011), we suggest evaluating the dynamic disequilibrium state of C cycle (e.g., Bloom *et al*., 2016), and further quantifying and reducing the SSA-induced uncertainty at large scales, especially with non-steady-state behavior, using this proposed framework.

4.3 Implications of SSA-induced uncertainty in MTT for C cycle research

As a key factor determining the ecosystem C sequestration capacity, the uncertainty of MTT tends to dominate the uncertainty in terrestrial ecosystem C sequestration (Friend *et al*., 2014; He *et al*., 2016). Thus, identifying the relative contribution of this highly uncertain ecosystem trait to C sequestration has become a hot topic in C cycle research (Todd-Brown *et al*., 2013; Carvalhais *et al*., 2014; Yan et al., 2017). We employed a systematic framework and quantified that the deviation in MTT when improperly invoking SSA directly results in a pronounced underestimation of ecosystem NEP (4.83-fold) in this large C uptake region. The substantial underestimation of NEP found is supported by Yu *et al*. (2014), who revealed that state-of-the-art process-based models under the SSA tended to underestimate NEP by five- to seven-fold relative to eddy covariance observations in eastern Asia monsoon subtropical forests. Moreover, process-based models significantly underestimated NEP compared to other approaches, e.g., biomass and soil inventory, and atmospheric inversion (Piao *et al*., 2009). This is mainly because the models consistently assume that the ecosystem has approached an

543 equilibrium state, which obviously neglects age-structure-related effects and underestimates
544 the turnover times at regional and global scales (Carvalhais *et al*., 2014; Yan *et al*., 2014;
545 Thurner *et al*., 2017).

546 Here, we firstly reveal that the deviation in ecosystem MTT induced by SSA has a
547 clearly decreasing relationship with increasing forest age. Furthermore, the biases in
548 vegetation allocation and turnover, rather than those in soil turnover, dominate the magnitude
549 of the deviation in MTT and its dependency on forest age. This finding is most likely due to
550 the significantly stronger relationship between vegetation C turnover and stand age, whereas
551 soil C turnover is mostly affected by climatic factors (Wang *et al*., 2018). In addition, the
552 vegetation C partition scheme varies with stand age (Zhou *et al*., 2013b). The decisive role of
553 whole-vegetation turnover time in determining the uncertainty in ecosystem C storage
554 capacity has been supported by recent modelling and experimental research (Friend *et al*.,
555 2014; Medlyn *et al*., 2015; Xue *et al*., 2017). Therefore, our results further highlight the need
556 to focus on the deviation in vegetation C turnover time under the SSA to avoid considerable
557 bias in ecosystem MTT and thus the C sequestration estimation.

558 The East Asian monsoon forest ecosystems represent one of the highest C uptake regions
559 worldwide, including mid- and high-latitude European and North American forests.
560 Particularly, the young age structure of forest stands in this region has been identified as a
561 major driver of the large NEP (Yu *et al*., 2014). Therefore, our result offers a significant
562 caveat for applying SSA in regions with a large portion of young ecosystems. We expect that
563 improved representations of forest age-driven growth and mortality into calibrated process-
564 based models will help reduce the aforementioned biases for the C balance of ecosystems
565 regionally and globally. Additionally, our finding on the age-dependent deviation of MTT
566 could also offer an opportunity to correct the MTT_OBS_I at regional or global scales (e.g.,

Thurner *et al*., 2016) with spatially-explicit forest age information, thereby providing a better benchmark to inform or parameterize C cycle models.

In addition to the uncertainty in the magnitude of C storage capacity, previous studies have revealed that the major uncertainty in the response of ecosystem C storage to climate arises from the uncertainty in the response of MTT to climate, which is 30% higher than that caused by NPP (Friend *et al*., 2014). However, to our knowledge, this is the first attempt to quantify the relationship between climate and ecosystem MTT in the disequilibrium state and to discuss the differences with that at the equilibrium state. Theoretically, an ecosystem at equilibrium is stable for a long time under the local climate (Luo and Weng, 2011); thus, a relatively strong correlation can be expected between the ecosystem MTT and climate. However, it is inappropriate to invoke the ideal SSA in ecosystems at dynamic disequilibrium, with the MTTs underestimated to a greater extent in young and middle-aged forests (by more than 50%) than mature forests (less than 20%). This age-induced inconsistency in MTT underestimations disturbs the actual spatial pattern of MTT and its covariance with climate, thereby leading to a decreased sensitivity of MTT to climate under the SSA. In contrast, the MTT_NSSA estimation based on long-term observational data in this study implicitly incorporated the age-structure-related effect on C cycle dynamics, thus providing a proper perspective on the actual correlation between MTT and climate. Currently, the contributions of climate-driven changes in C turnover times to C storage are usually underestimated in modelling studies (Hararuk *et al*., 2015; Koven *et al*., 2015, 2017). Therefore, the substantial underestimation we revealed in sensitivities of MTT to temperature and precipitation induced by the SSA calls for more attention in future C-climate feedback research. Under global warming and changes in precipitation regimes (IPCC, 2013), the underestimated response of MTT to climate will apparently underestimate the spatial and temporal changes in MTT, thereby underestimating the change in predicted global NEP. Here the exchange of space for

time to interpret the sensitivity of MTT to climate could cause some degree of bias, as such inference cannot include certain processes like acclimation of microbial respiration to warming or shifts in plant species over time (e.g., Koven *et al*., 2017; Yan *et al*., 2017). Nonetheless, the present-day spatial correlation between climate and MTT approximated the temporal correlation between these variables (Fig. S5) and well supported this inference.

4.4 Advantages and challenges of C cycle MDF based on long-term data

Carbon turnover times and C cycle dynamics are always model-dependent because of the difficulty obtaining them from observations alone under the NSSA (Sierra *et al*., 2017). However, even the state-of-the-art models fail to accurately capture the observed C allocations and turnover processes, resulting in high uncertainties in C dynamic simulations (De Kauwe *et al*., 2014; Negrón-Juárez *et al*., 2015). Therefore, applying MDF technology to constrain these C states and processes becomes important for accurately estimating MTT and C sequestration in the disequilibrium state (Bloom *et al*., 2016).

The uncertainties in the current ecosystem MTT and C sequestration estimates mainly result from the lack of initial state of the C pools and inaccurate model parameters (Bellassen *et al*., 2011; Wang *et al*., 2011), because C cycle modelling typically relies on pre-arranged parameters retrieved from literature, prescribed PFT or spin-up processes (Exbrayat *et al*., 2014; Zhou *et al*., 2013b). In this study, the long-term and multi-source observations combined with a series of experimental constraints directly provided the initial values of the corresponding C pools and better constrained the NSSA parameters and dynamic C pool trajectories (Smallman et al., 2017; Bloom and Williams, 2015), thus substantially reducing the uncertainties arising from the SSA and limited data. Furthermore, insights into the underlying mechanisms that regulate the ecosystem C cycle can be provided based on the key process parameters, which are difficult to obtain from observations without SSA. For example,

we might explore how the C allocation and turnover in live and dead C respond to climate, thereby regulating the response of the whole-ecosystem MTT to climate (Fig. S6).

The uncertainty from the model structure and observational data also induce errors in the estimations of ecosystem MTT and C sequestration (Ahlström *et al*., 2012). However, as this study aimed to compare the differences in MTTs estimated under different hypotheses with the same model and data, these two factors would not undermine the main conclusions. When applied at the regional scale, some external disturbances such as fire and land-use change (Erb, 2016); vegetation mortality dynamics affected by drought, insect pests, and frost (Thurner *et al*., 2016); as well as the dynamic scheme of C allocation limited by resources availability (Xia *et al*. 2015) should be added to the model. Although the model without moisture effect did not significantly affect the results in these forests (Table S7), the explicit representation of moisture effect may improve the model simulation when applied at large scales. Besides, more underground process observations should be added in future research to better constrain the corresponding parameters, e.g., θ_{min}, reflecting the decomposition of litter into soil.

In this study, we provided insights into the large biases associated with the improper application of the SSA, causing considerable underestimation in the magnitudes of MTT and its sensitivities to climate, and spatiotemporal variations in ecosystem C sequestration. Our findings on the age-dependent uncertainty in MTT provide significant implications for the implementation of mitigation policies for regional to global ecosystems with substantial young plantations. Moreover, the MDF framework we developed has the potential to facilitate future model intercomparisons, benchmarking and optimization at large scales, as well as to effectively quantify and then reduce the uncertainty in ecosystem C sequestration by estimating MTT in the disequilibrium state with long-term and multi-source observations.

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References

Ahlström, A., Schurgers, G., Arneth, A., & Smith, B. (2012). Robustness and uncertainty in terrestrial ecosystem carbon response to CMIP5 climate change projections. *Environmental Research Letters, 7*(4), 044008.

Anav, A., Friedlingstein, P., Kidston, M., Bopp, L., Ciais, P., Cox, P., ... & Zhu, Z. (2013). Evaluating the land and ocean components of the global carbon cycle in the CMIP5 Earth System Models. *Journal of Climate*, *26*(18), 6801-6843.

Barrett, D. J. (2002). Steady state turnover time of carbon in the Australian terrestrial biosphere. *Global Biogeochemical Cycles*, *16*(4), 55-1–55-21.

Bellassen, V., Delbart, N., Le Maire, G., Luyssaert, S., Ciais, P., & Viovy, N. (2011). Potential knowledge gain in large-scale simulations of forest carbon fluxes from remotely sensed biomass and height. *Forest ecology and management*, *261*(3), 515-530.

Bloom, A. A., & Williams, M. (2015). Constraining ecosystem carbon dynamics in a data-limited world: integrating ecological" common sense" in a model-data fusion framework. *Biogeosciences, 12*(5), 1299-1315.

Bloom, A. A., Exbrayat, J. F., Ir, V. D. V., Feng, L., & Williams, M. (2016). The decadal state of the terrestrial carbon cycle: global retrievals of terrestrial carbon allocation, pools, and residence times. *Proceedings of the National Academy of Sciences, 113*(5), 1285-1290.

Bolin, B., & Rodhe, H. (1973). A note on the concepts of age distribution and transit time in natural reservoirs. *Tellus, 25*(1), 58-62.

Carvalhais, N., Forkel, M., Khomik, M., Bellarby, J., Jung, M., Migliavacca, M., ... & Weber, U. (2014). Global covariation of carbon turnover times with climate in terrestrial ecosystems. *Nature, 514*(7521), 213-217.

Carvalhais, N., Reichstein, M., Ciais, P., Collatz, G. J., Mahecha, M. D., Montagnani, L., ... & Seixas, J. (2010). Identification of vegetation and soil carbon pools out of equilibrium in a process model via eddy covariance and biometric constraints. *Global Change Biology, 16*(10), 2813-2829.

Carvalhais, N., Reichstein, M., Seixas, J., Collatz, G. J., Pereira, J. S., Berbigier, P., ... & Rambal, S. (2008). Implications of the carbon cycle steady state assumption for biogeochemical modeling performance and inverse parameter retrieval. *Global Biogeochemical Cycles, 22*(2), 1081-1085.

Chen, G. S., Yang, Y. S., Ping-Ping, L., & Zhang, Y. P. (2008). Regional patterns of soil respiration in china's forests. *Acta Ecologica Sinica, 28*(4):1748-1761.

Chen, S., Huang, Y., Zou, J. and Shi, Y. (2013). Mean residence time of global topsoil organic carbon depends on temperature, precipitation and soil nitrogen. *Global and Planetary Change, 100,* 99-108.

Galbraith, D., Malhi, Y., Affum-Baffoe, K., Castanho, A. D., Doughty, C. E., Fisher, R. A., ... & Sonké, B. (2013). Residence times of woody biomass in tropical forests. *Plant Ecology & Diversity*, *6*(1), 139-157.

De Kauwe, M. G., Medlyn, B. E., Zaehle, S., Walker, A. P., Dietze, M. C., Wang, Y. P., ... & Wårlind, D. (2014). Where does the carbon go? A model–data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free‐air CO2 enrichment sites. *New Phytologist, 203*(3), 883-899.

Exbrayat, J. F., Pitman, A. J., & Abramowitz, G. (2014). Response of microbial decomposition to spin-up explains CMIP5 soil carbon range until 2100. *Geoscientific Model Development, 7*(6), 2683-2692.

Fox, A., Williams, M., Richardson, A. D., Cameron, D., Gove, J. H., Quaife, T., ... & Van Wijk, M. T. (2009). The REFLEX project: comparing different algorithms and implementations for the inversion of a terrestrial ecosystem model against eddy covariance data. *Agricultural and Forest Meteorology, 149*(10), 1597-1615.

Frank, D. A., Pontes, A. W. and McFarlane, K. J. (2012). Controls on soil organic carbon stocks and turnover among North American ecosystems. *Ecosystems*, *15*(4), 604-615

Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., ... & Bala, G. (2006). Climate–carbon cycle feedback analysis: results from the C^4MIP model intercomparison. *Journal of climate*, *19*(14), 3337-3353.

Friend, A. D., Lucht, W., Rademacher, T. T., Keribin, R., Betts, R., Cadule, P., ... & Ito, A. (2014). Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO_2. *Proceedings of the National Academy of Sciences of the United States of America, 111*(9), 3280-3285.

Gill, R. A. and Jackson, R. B. (2000). Global patterns of root turnover for terrestrial ecosystems. *The New Phytologist*, *147*(1), 13-31.

Goulden, M. L., McMillan, A. M. S., Winston, G. C., Rocha, A. V., Manies, K. L., Harden, J. W., & Bond‐Lamberty, B. P. (2011). Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. *Global Change Biology, 17*(2), 855-871.

Hararuk, O., Smith, M. J., & Luo, Y. (2015). Microbial models with data-driven parameters predict stronger soil carbon responses to climate change. *Global Change Biology, 21*(6), 2439–2453.

He, Y., Trumbore, S. E., Torn, M. S., Harden, J. W., Vaughn, L. J., Allison, S. D., & Randerson, J. T. (2016). Radiocarbon constraints imply reduced carbon uptake by soils during the 21st century. *Science, 353*(6306), 1419-1424.

Huang, S., Arain, M. A., Arora, V. K., Yuan, F., Brodeur, J., & Peichl, M. (2011). Analysis of nitrogen controls on carbon and water exchanges in a conifer forest using the CLASS-CTEMN+ model. *Ecological modelling, 222*(20-22), 3743-3760.

IPCC, 2013: Climate Change 2013: The Physical Science Basis. Contribution of Working Group 1 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Stocker, T. F., D. Qin, G.‐K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley (Eds.). Cambridge University Press, Cambridge, UK.

Ji, J. J. (1995). A climate-vegetation interaction model: Simulating physical and biological processes at the surface, *Journal of Biogeography, 22,* 2063 – 2069, doi:10.2307/2845941.

Karhu, K., Fritze, H., Tuomi, M., Vanhala, P., Spetz, P., Kitunen, V., & Liski, J. (2010). Temperature sensitivity of organic matter decomposition in two boreal forest soil profiles. *Soil Biology and Biochemistry, 42*(1), 72-82.

Koven, C. D., Chambers, J. Q., Georgiou, K., Knox, R., Negron-Juarez, R., Riley, W. J., ... & Jones, C. D. (2015). Controls on terrestrial carbon feedbacks by productivity versus turnover in the CMIP5 Earth System Models. *Biogeosciences, 12*(17), 5211-5228.

Koven, C. D., Hugelius, G., Lawrence, D. M., & Wieder, W. R. (2017). Higher climatological temperature sensitivity of soil carbon in cold than warm climates. *Nature Climate Change, 7*(11), 817-822.

Law, B. E., Thornton, P. E., Irvine, J., Anthoni, P. M., & Van, T. S. (2001). Carbon storage and fluxes in ponderosa pine forests at different developmental stages. *Global Change Biology, 7*(7), 755-777.

Le Quéré, C., Andrew, R. M., Friedlingstein, P., Sitch, S., Pongratz, J., Manning, A. C., ... & Boden, T. A. (2018). Global Carbon Budget 2017. *Earth System Science Data, 10*(1), 405-448.

Le Toan, T., Quegan, S., Davidson, M. W. J., Balzter, H., Paillou, P., Papathanassiou, K., ... & Ulander, L. (2011). The BIOMASS mission: Mapping global forest biomass to better understand the terrestrial carbon cycle. *Remote sensing of environment, 115*(11), 2850-2860.

Li, C., He, H. L., Liu, M., Su, W., Fu, Y. L., Zhang, L. M., ... & Yu, G. R. (2008). The design and application of CO2 flux data processing system at ChinaFLUX. *Geo-Information Science, 10*(5), 557-565.

Li, X. J., Zhou, T., & He, X. Z. (2009). Carbon sink of forest ecosystem driven by NPP increasing in China. *Journal of Natural Resources, 24*(3), 491-497.

Liu, H., Tang, L. Q., Hu. B., Liu, G. R., Wang, Y. S., Bai, F., ... & Zhu, Y. J. (2017a). Photosynthetically active radiation dataset in Chinese Ecosystem Research Network (2005 – 2015). *China Scientific Data, 2*(1), 1-10.

Liu, Y., He, N., Zhu, J., Xu, L., Yu, G., Niu, S., ... & Wen, X. (2017b). Regional variation in the temperature sensitivity of soil organic matter decomposition in China's forests and grasslands. *Global change biology, 23*(8), 3393-3402.

Lugo, A. E., & Brown, S. (1986). Steady state terrestrial ecosystems and the global carbon cycle. *Vegetatio, 68*(2), 83-90.

752 Luo, Y., & Weng, E. (2011). Dynamic disequilibrium of the terrestrial carbon cycle under global
753 change. *Trends in Ecology & Evolution, 26*(2), 96-104.
754 Luo, Y., Shi, Z., Lu, X., Xia, J., Liang, J., Jiang, J., ... & Chen, B. (2017). Transient dynamics of
755 terrestrial carbon storage: mathematical foundation and numeric examples. *Biogeosciences,*
756 *14*(1), 145-161.
757 Luo, Y., White, L. W., Canadell, J. G., DeLucia, E. H., Ellsworth, D. S., Finzi, A., ... & Schlesinger,
758 W. H. (2003). Sustainability of terrestrial carbon sequestration: a case study in Duke Forest with
759 inversion approach. *Global biogeochemical cycles, 17*(1), 1021. DOI: 10.1029/2002GB001923.
760 Luyssaert, S., Schulze, E. D., Börner, A., Knohl, A., Hessenmöller, D., Law, B. E., ... & Grace, J.
761 (2008). Old-growth forests as global carbon sinks. *Nature, 455*(7210), 213-215.
762 Mantgem, P. J. V., Stephenson, N. L., Byrne, J. C., Daniels, L. D., Franklin, J. F., Fulé, P. Z., ... &
763 Veblen, T. T. (2009). Widespread increase of tree mortality rates in the western united states.
764 *Science, 323*(5913), 521-524.
765 Manzoni, S., and A. Porporato (2009). Soil carbon and nitrogen mineralization: Theory and models
766 across scales. *Soil Biology and Biochemistry, 41*(7), 1355-1379.
767 Medlyn, B. E., Zaehle, S., De Kauwe, M. G., Walker, A. P., Dietze, M. C., Hanson, P. J., ... &
768 Prentice, I. C. (2015). Using ecosystem experiments to improve vegetation models. *Nature*
769 *Climate Change, 5*(6), 528-534.
770 Mi, N., Yu, G., Wang, P., Wen, X. and Sun, X., 2006. A preliminary study for spatial representiveness
771 of flux observation at ChinaFLUX sites. *Sci. China Ser. D-Earth Sci., 49*(2): 24-35.
772 Morales, P., Sykes, M. T., Prentice, I. C., Smith, P., Smith, B., Bugmann, H., ... & Sánchez, A. (2005).
773 Comparing and evaluating process‐based ecosystem model predictions of carbon and water
774 fluxes in major European forest biomes. *Global Change Biology, 11*(12), 2211-2233.
775 Negrón-juárez, R. I., Koven, C. D., Riley, W. J., Knox, R. G., & Chambers, J. Q. (2015). Observed
776 allocations of productivity and biomass, and turnover times in tropical forests are not accurately
777 represented in cmip5 earth system models. *Environmental Research Letters, 10*(6), 064017.
778 Odum, E. P. (1966). The strategy of ecosystem development. *Science, 164*, 262–270.
779 Pan, Y. D., Birdsey, R. A., Fang, J. Y., Houghton, R., Kauppi, P. E., Kurz, W. A., …Hayes, D. (2011).
780 A large and persistent carbon sink in the world's forests. *Science, 333*, 988–993.
781 Piao, S., Fang, J., Ciais, P., Peylin, P., Huang, Y., Sitch, S., & Wang, T. (2009). The carbon balance of
782 terrestrial ecosystems in china. *Nature, 458*(7241), 1009-1013.
783 Piao, S., Luyssaert, S., Ciais, P., Janssens, I. A., Chen, A., Cao, C., ... & Wang, S. (2010). Forest
784 annual carbon cost: a global-scale analysis of autotrophic respiration. *Ecology, 91*(3), 652-661.
785 Pietsch, S. A., & Hasenauer, H. (2006). Evaluating the self‐initialization procedure for large‐scale
786 ecosystem models. *Global Change Biology, 12*(9), 1658-1669.
787 Post, W. M., J. Pastor, P. J. Zinke, and A. G. Stangenberger (1985). Global patterns of soil nitrogen
788 storage, *Nature, 317*(6038), 613 – 616, doi:10.1038/317613a0.
789 Reich, P. B., Luo, Y. J., Bradford, J. B., Poorter, H., Perry, C. H., & Oleksyn, J.(2014). Temperature
790 drives global patterns in forest biomass distribution in leaves, stems, and roots. *Proceedings of*
791 *the National Academy of Sciences of the United States of America, 111*(38), 13721–13727.
792 Richardson, A. D., Williams, M., Hollinger, D. Y., Moore, D. J., Dail, D. B., Davidson, E. A., ... &
793 Rodrigues, C. (2010). Estimating parameters of a forest ecosystem c model with measurements of
794 stocks and fluxes as joint constraints. *Oecologia, 164*(1), 25-40.
795 Rodhe, H. (1978). Budgets and turn-over times of atmospheric sulfur compounds. *Sulfur in the*
796 *Atmosphere, 12*(1-3), 671-680.
797 Safta, C., Ricciuto, D. M., Sargsyan, K., Debusschere, B., Najm, H. N., Williams, M., & Thornton, P.
798 E. (2015). Global sensitivity analysis, probabilistic calibration, and predictive assessment for the
799 data assimilation linked ecosystem carbon model. *Geoscientific Model Development Discussions,*
800 *8*(7), 6893-6948.
801 Sanderman, J., Amundson, R. G. and Baldocchi, D. D. (2003). Application of eddy covariance
802 measurements to the temperature dependence of soil organic matter mean residence time. *Global*
803 *Biogeochemical Cycles, 17*(2), 30-1.
804 Schwartz, S. E. (1979). Residence times in reservoirs under non-steady-state conditions: application to
805 atmospheric so2 and aerosol sulfate1. *Tellus, 31*(6), 530-547.

Sierra, C. A., Müller, M., Metzler, H., Manzoni, S., & Trumbore, S. E. (2017). The muddle of ages, turnover, transit, and residence times in the carbon cycle. *Global Change Biology, 23*(5), 1763-1773.

Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., ... & Thonicke, K. (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology, 9*(2), 161-185.

Smallman, T. L., Exbrayat, J. F., Mencuccini, M., Bloom, A. A., & Williams, M. (2017). Assimilation of repeated woody biomass observations constrains decadal ecosystem carbon cycle uncertainty in aggrading forests. *Journal of Geophysical Research: Biogeosciences, 122*(3), 528-545.

Strand, A. E., Pritchard, S. G., McCormack, M. L., Davis, M. A., & Oren, R. (2008). Irreconcilable differences: fine-root life spans and soil carbon persistence. *Science, 319*(5862), 456-458.

Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An overview of cmip5 and the experiment design. *Bulletin of the American Meteorological Society, 93*(4), 485-498.

Thurner, M., Beer, C., Carvalhais, N., Forkel, M., Santoro, M., Tum, M., & Schmullius, C. (2016). Large-scale variation in boreal and temperate forest carbon turnover rate is related to climate. *Geophysical Research Letters,43*(9), 4576-4585.

Thurner, M., Beer, C., Ciais, P., Friend, A. D., Ito, A., Kleidon, A., ... & Tum, M. (2017). Evaluation of climate-related carbon turnover processes in global vegetation models for boreal and temperate forests. *Global Change Biology, 23*(8), 3076-3091.

Todd-Brown, K. E. O., Randerson, J. T., Post, W. M., Hoffman, F. M., Tarnocai, C., Schuur, E. A. G., & Allison, S. D. (2013). Causes of variation in soil carbon simulations from CMIP5 Earth system models and comparison with observations. *Biogeosciences, 10*(13), 1717–1736.

Trumbore, S. (2006). Carbon respired by terrestrial ecosystems–recent progress and challenges. *Global Change Biology, 12*(2), 141-153.

Wang, J., Sun, J., Xia, J., He, N., Li, M., & Niu, S. (2018). Soil and vegetation carbon turnover times from tropical to boreal forests. *Functional Ecology, 32*(1), 71-82.

Wang, W., Dungan, J., Hashimoto, H., Michaelis, A. R., Milesi, C., Ichii, K., & Nemani, R. R. (2011). Diagnosing and assessing uncertainties of the carbon cycle in terrestrial ecosystem models from a multi-model ensemble experiment. *Global Change Biology, 17*(3), 1350-1366.

Williams, M., Schwarz, P. A., Law, B. E., Irvine, J., & Kurpius, M. R. (2005). An improved analysis of forest carbon dynamics using data assimilation. *Global Change Biology, 11*(1), 89-105.

Wutzler, T., & Reichstein, M. (2007). Soils apart from equilibrium? consequences for soil carbon balance modelling. *Biogeosciences, 4*, 125–136.

Xia, J., Chen, Y., Liang, S., Liu, D., & Yuan, W. (2015). Global simulations of carbon allocation coefficients for deciduous vegetation types. *Tellus Series B-chemical & Physical Meteorology, 67*(2), 28016.

Xia, J., Luo, Y., Wang, Y. P., & Hararuk, O. (2013). Traceable components of terrestrial carbon storage capacity in biogeochemical models. *Global Change Biology, 19*(7), 2104-2116.

Xu T, White L, Hui D, Luo Y. (2006). Probabilistic inversion of a terrestrial ecosystem model: Analysis of uncertainty in parameter estimation and model prediction. *Global Biogeochemical Cycles, 20*(2), doi:10.1029/2005GB002468.

Xue, B. L., Guo, Q., Hu, T., Xiao, J., Yang, Y., Wang, G., ... & Zhao, X. (2017). Global patterns of woody residence time and its influence on model simulation of aboveground biomass. *Global Biogeochemical Cycles, 31*(5), 821-835.

Yan, Y., Luo, Y., Zhou, X., & Chen, J. (2014). Sources of variation in simulated ecosystem carbon storage capacity from the 5th Climate Model Intercomparison Project (CMIP5). *Tellus B: Chemical and Physical Meteorology, 66*(1), 22568.

Yan, Y., Zhou, X., Jiang, L., & Luo, Y. (2017). Effects of carbon turnover time on terrestrial ecosystem carbon storage. *Biogeosciences, 14*(23), 5441.

Yu, G., Chen, Z., Piao, S., Peng, C., Ciais, P., Wang, Q., ... & Zhu, X. (2014). High carbon dioxide uptake by subtropical forest ecosystems in the East Asian monsoon region. *Proceedings of the National Academy of Sciences, 111*(13), 4910-4915.

Zaehle, S., Sitch, S., Prentice, I. C., Liski, J., Cramer, W., Erhard, M., ... & Smith, B. (2006). The importance of age‐related decline in forest NPP for modeling regional carbon balances. *Ecological Applications, 16*(4), 1555-1574.

Zhang, C., Ju, W., Chen, J. M., Li, D., Wang, X., Fan, W., ... & Zan, M. (2014). Mapping forest stand age in China using remotely sensed forest height and observation data. *Journal of Geophysical Research: Biogeosciences, 119*(6), 1163-1179.

Zhang, L., Luo, Y., Yu, G., & Zhang, L. (2010). Estimated carbon residence times in three forest ecosystems of eastern China: Applications of probabilistic inversion. *Journal of Geophysical Research: Biogeosciences, 115*(G1) :137-147.

Zhang, X., & Wu, K. (2001). Fine-root production and turnover for forest ecosystems. *Scientia Silvae Sinicae*, *37*(3), 126-138.

Zheng, Z. M., Yu, G. R., Sun, X. M., Li, S. G., Wang, Y. S., Wang, Y. H., ... & Wang, Q. F. (2010). Spatio-temporal variability of soil respiration of forest ecosystems in China: influencing factors and evaluation model. *Environmental management, 46*(4), 633-642.

Zhou, G., Liu, S., Li, Z., Zhang, D., Tang, X., Zhou, C., ... & Mo, J. (2006). Old-growth forests can accumulate carbon in soils. *Science, 314*(5804), 1417-1417.

Zhou, G., Peng, C., Li, Y., Liu, S., Zhang, Q., Tang, X., ... & Chu, G. (2013a). A climate change‐induced threat to the ecological resilience of a subtropical monsoon evergreen broad‐leaved forest in Southern China. *Global Change Biology, 19*(4), 1197-1210.

Zhou, T., & Luo, Y. (2008). Spatial patterns of ecosystem carbon residence time and NPP‐driven carbon uptake in the conterminous United States. *Global Biogeochemical Cycles, 22*(3), 3411-3434.

Zhou, T., Shi, P., Jia, G., & Luo, Y. (2013b). Nonsteady state carbon sequestration in forest ecosystems of china estimated by data assimilation. *Journal of Geophysical Research Biogeosciences, 118*(4), 1369-1384.

Zhou, T., Shi, P., Jia, G., Li, X., & Luo, Y. (2010). Spatial patterns of ecosystem carbon residence time in Chinese forests. *Science China Earth Sciences, 53*(8), 1229-1240.

Zhu, G., Ju, W., Chen, J. M., Gong, P., Xing, B., & Zhu, J. (2012). Foliage clumping index over China's landmass retrieved from the MODIS BRDF parameters product. *IEEE Transactions on Geoscience and Remote Sensing, 50*(6), 2122-2137.

Zobitz, J., A. Desai, D. Moore, and M. Chadwick (2011), A primer for data assimilation with ecological models using Markov Chain Monte Carlo (MCMC). *Oecologia, 167*(3), 599–611.

Figure captions

Figure 1. Map showing the distribution of 10 forest ecosystems in the Chinese Ecosystem Research Network (CERN). BNF: Xishuangbanna tropical seasonal rainforest, HSF: Heshan subtropical evergreen broad-leaved forest, DHF: Dinghu Mountain subtropical evergreen coniferous and broad-leaved mixed forest, ALF: Ailao subtropical evergreen broad-leaved forest, QYF: Qianyanzhou subtropical evergreen artificial coniferous mixed forest, HTF: Huitong subtropical evergreen broad-leaved forest, SNF: Shennongjia subtropical evergreen deciduous broad-leaved mixed forest, MXF: Maoxian warm temperate deciduous coniferous mixed forest, BJF: Beijing warm temperate deciduous broad-leaved mixed forest, CBF: Changbai Mountain temperate deciduous coniferous and broad-leaved mixed forest.

Figure 2. Structures of the Data Assimilation Linked Ecosystem Carbon (DALEC)-evergreen model (grey) and the DALEC-deciduous model (grey and black). Dotted arrows show the inputs into the photosynthesis model.

Figure 3. Flow chart of the model data fusion framework under the steady state assumption (SSA) and non-steady state assumption (NSSA).

Figure 4. Optimized key parameters involved in the allocation and turnover processes under the non-steady state assumption (NSSA) and steady state assumption (SSA) at 10 sites along a decreasing latitudinal gradient. The black and grey boxes denote NSSA and SSA, respectively.

908 Figure 5. Comparisons between the observed and modelled values at all sites under the non-steady
909 state (NSSA: black dots) and steady state (SSA: red dots) assumptions
910 Figure 6. Magnitude of ecosystem C turnover times under the equilibrium and disequilibrium
911 hypotheses. The black, light-grey, and dark grey boxes denote the inversion-based MTT under
912 non-steady state (MTT_NSSA_O), inversion-based MTT under steady state (MTT_SSA_I), and
913 observation-based MTT under steady state (MTT_OBS_I), respectively.
914 Figure 7. Relationships between forest age and differences of the entire-ecosystem MTT (ΔMTT) as
915 well as wood turnover rates ($\Delta\theta_{woo}$) estimated under the steady state assumption (SSA) and non-
916 steady state assumption (NSSA) hypotheses.
917 Figure 8. Associations of mean carbon turnover times with temperature and precipitation under the
918 steady state assumption (SSA, grey triangles) and non-steady state assumption (NSSA, black
919 dots).
920 Figure 9. Comparison of net ecosystem productivity (NEP) estimated with the parameters inverted
921 under the steady state assumption (SSA) and non-steady state assumption (NSSA) in 10 forest
922 ecosystems of different ages